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Evolution of Cooperation: Two for One?

Dispatch

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How can cooperation thrive in a selfish world? Recent evolution experiments show how bacteria themselves can generate conditions that make cooperation a winning strategy. At least in the short term.

Cooperation is ubiquitous at many levels of biological organization. Genes within a cell cooperate to replicate in a coordinated manner; cells within multicellular organisms act together to build a functioning soma; animals within social groups cooperate to forage and reproduce. Although cooperation is pervasive, it is not trivial to understand how it evolves. Many cooperative acts are evolutionarily derived characters, and thus we have to understand how a cooperator produced by spontaneous mutation could spread in an ancestral population of non-cooperating individuals. Recent studies by Rainey and Rainey [1] and Velicer and Yu [2] have shed new light on how this might happen.

Cooperation is difficult to evolve because of its very nature. Its defining aspect is the investment of resources toward a public good, and thus the adoption of a costly strategy that can benefit other individuals, regardless of whether those other individuals contribute to the public good or not [3]. A newly emerging cooperator would thus improve the situation of the community, but carry the costs alone and thus be unable to thrive. The prevalence of cooperation in nature, however, suggests that there are solutions to this dilemma, and at least parts of these solutions are known. One key idea is that rare cooperators, perhaps the progeny of a single cooperative mutant, interact more often with one another than with non-cooperating residents [4]. The benefits from cooperation remain thereby confined to the initially small group of cooperators, and help this group to prosper.

How can cooperators interact preferentially with one another? Two common explanations exist. First, cooperators can recognize other cooperators or relatives, which are likely to be cooperators as well. Although such discrimination has been demonstrated, even for microbes [5], its requirements are substantial and probably often not fulfilled. Alternatively, individuals do not recognize one another, but relatives remain spatially close and thus interact preferentially. This requires that the physical environment is structured so that the dispersal of newborn individuals is limited. It is not clear how often natural environments fulfill this condition. The new papers by Rainey and Rainey [1] and Velicer and Yu [2], both reporting experimental studies on cooperation in microbes, suggest a new and simpler solution.

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Rainey and Rainey [1] report how cooperative groups of bacteria colonize a new niche in their laboratory environment. They evolved experimental populations of the plant pathogen *Pseudomonas fluorescens* in static broth microcosms — unshaken glass beakers containing growth medium. The experiments were initiated with wild-type cells that inhabited the liquid phase of the medium and thus suffered from oxygen limitation. About two days after the start of the experiment, the authors consistently recorded the emergence of cells with a new phenotype — the so-called 'wrinkly spreaders' — which were able to overcome oxygen limitation by colonizing the air–broth interface.

This colonization was made possible by the overproduction of an adhesive polymer, causing the cells to adhere firmly to one another and to surfaces. Adhesion allowed the formation of a self-supporting mat at the surface of the broth, providing the cells with access to both oxygen and nutrients. The evolved trait is a cooperative act because the mat is a common good that allows all its inhabitants to gain access to oxygen, irrespective of whether they contribute to the mat or not. This has important consequences for the fate of the cooperative group, as will be discussed below.

Velicer and Yu [2] studied cooperative motility in experimental populations of the bacterium *Myxococcus xanthus*. Wild-type strains of this soil-dwelling predator swarm in groups across soft surfaces by a mechanism known as 'S-motility'. At the beginning of the experiment, the experimenters incapacitated S-motility by knocking out the *pilA* gene, leading to the loss of the type IV pili. Populations of this mutant were then allowed to evolve under conditions that imposed strong selection for motility; only cells that made it to the edge of a growing colony had a chance of surviving to the next generation. The question then was: would the cells regain some of the motility that they lost through the knockout mutation? Indeed they did: after only 32 rounds of selection, all eight populations showed increases in motility.

While the amount of increase was substantial in all cases, in two populations it was dramatic. Closer examination revealed that these two strains had recruited another motility mechanism that is normally not suited for soft surfaces, the 'A-motility'. In this type of motility, propulsion is thought to occur through the extrusion of slime. Modification of the A-motility alone, however, did not explain all of the regained motility. Both strains showed increased production of fibrils, forming an extracellular matrix consisting of carbohydrates and proteins. This matrix was essential for the regained motility, perhaps by increasing the efficiency of the A-motility on the soft surface. Interestingly, the presence of the matrix increased motility of all cells in a colony, irrespective of whether they contributed to it or not. Fibril production was therefore a cooperative act. At the same time, fibrils triggered

cohesion between fibril-producers, leading to clusters of cells that shared the derived trait.

These new studies [1,2] are noteworthy because the cellular change that brought about the cooperative act in both cases also increased cohesion. Cohesion can promote the attachment of daughter cells to each other and can act as a mechanism to create clusters of cells in an otherwise well-mixed population, such as in the liquid cultures of Rainey and Rainey [1]. *Myxococcus* cells live on surfaces and not in a liquid habitat, but their motility in the absence of cohesion would also create random distributions in a two-dimensional world. Thus, with cohesion, a single trait both confers cooperation and increases the probability of preferential interactions. Note that, in earlier explanations for the evolution of cooperation, the cooperative act and mechanism for preferential interaction were two separate traits. With cohesion, we get two adaptations for one trait.

Of course, cohesion alone is a simple and imperfect solution. Rainey and Rainey [1] note that the mats quickly become infested with cells that do not overproduce polymers. Such 'cheater' cells do not pay the cost and yet benefit by gaining access to oxygen. The added mass of cheaters eventually sinks the mat. Thus simple cohesion is imperfect, because it is vulnerable to cheating, which in this case eventually destroys the community. The evolution of cooperative groups, albeit transient, is nevertheless critical, because it sets the potential for additional evolutionary changes. The cooperators could evolve a less expensive mechanism for producing polymers. Alternatively, they could evolve to enhance the benefits of cooperation.

A critical change, for example, might be the evolution of cohesion specificity. That would require the evolution of a polymer that preferentially binds to itself. As a consequence, cells not producing polymers would be excluded from the group. In another social microbe, the cellular slime mold *Dyctyostelium discoideum* [5], cohesion specificity has evolved through a receptor that binds to itself. These postulated evolutionary changes could help to make the system more robust by decreasing the cost cheaters impose on the system (the cheating load). Once a robust system is well established, new cooperative traits could be added. Most importantly, the evolution of such new traits would not be problematic, because cohesion that would direct the benefits of cooperation to cooperators is already present. The road to more complex cooperative systems would then be paved by evolving new cooperative traits layered over the original cooperative trait that was seeded by cohesion.

Up to now, we have made no distinction between 'minimal' cooperation and 'synergistic' cooperation. Minimal cooperation is simply a contribution to the common good and has been demonstrated directly in both studies. Synergism is a special case of cooperation: the situation where a group of individuals gain some benefit together that they could not obtain alone [3]. With synergism, groups can achieve previously unattainable functions and possibilities, an effect that may have driven some of the major evolutionary transitions [7]. Both of the new studies [1,2] indicate that the microbes in their experiments may interact synergistically, but they do not prove it. The relevant question is: can the surface of the microcosm used by Rainey and Rainey [2] only be colonized by groups, but not by individual wrinkly spreaders? And, likewise, is the modified motility system of *M. xanthus* [2] only effective in groups? These questions could be addressed experimentally. Demonstrating synergism would strengthen the viewpoint that these undifferentiated clusters of microbes indeed reached new levels of biological organization.

The new studies [1,2] provide a possible solution to the paradox of requiring simultaneously two independent traits — the cooperative act and the preferential interaction among cooperators — for the evolution of cooperation. In hindsight, such a simple solution should have been obvious. Why pay for two when you can get two for the price of one? The very simplicity of the solution, however, may have been its downfall. We are attracted to complexity because we are not challenged by simplicity. Fortunately, evolution does not care.

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